Integrated study of benthic foraging resources for Atlantic walrus (Odobenus rosmarus rosmarus) in the Pechora Sea, southeastern Barents Sea

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Integrated study of benthic foraging resources for Atlantic walrus (*Odobenus rosmarus rosmarus*) in the Pechora Sea, south-eastern Barents Sea

Anna Gebruk[1,2] | Polina Mikhaylyukova[1,3] | Maria Mardashova[1] | Varvara Semenova[4] | Lea-Anne Henry[2] | Nikolay Shabalin[1] | Bhavani E. Narayanaswamy[5] | Vadim Mokievsky[6]

[1]Lomonosov Moscow State University Marine Research Center, Moscow, Russia

[2]School of GeoSciences, University of Edinburgh, Edinburgh, UK

[3]Geography Department, Lomonosov Moscow State University, Moscow, Russia

[4]Marine Mammal Research and Expedition Center, Moscow, Russia

[5]The Scottish Association for Marine Science, Oban, UK

[6]Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia

Correspondence
Anna Gebruk, University of Edinburgh, Grant Institute, Room 349, The King's Buildings, James Hutton Road, Edinburgh, EH9 3FE, UK.
Email: Anna.Gebruk@ed.ac.uk

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Abstract

1. The Atlantic walrus, *Odobenus rosmarus rosmarus*, forms a herd of nearly 4,000 heads in the Pechora Sea (south-eastern Barents Sea). The Near Threatened status of *O. rosmarus rosmarus* and the relative isolation of the Pechora Sea population, as well as the potential impacts of human activities in the area, make it important to characterize key habitats, including feeding grounds, in order to protect the species.
2. The aim of the present study was to integrate multiple sources of environmental and biological data collected by satellite telemetry, remotely operated vehicle (ROV), and benthic grab sampling to examine the distribution and diversity of benthic foraging resources used by walrus in the Pechora Sea.
3. Analysis of satellite telemetry data from seven males tagged on Vaigach Island helped to identify areas of high use by walruses near haulout sites on Matveev and Vaigach islands, and in between. Field data were collected from those feeding grounds in July 2016 using ROV video recordings and bottom grab sampling. Analysis of 19 grab stations revealed a heterogeneous macrobenthic community of 133 taxa with a mean biomass of 147.11 ± 7.35 g/m^2. Bivalve molluscs, particularly *Astarte borealis*, *Astarte montagui*, and *Ciliatocardium ciliatum*, dominated the overall macrobenthic biomass, making up two-thirds of the total.
4. Analysis of 16 ROV video transects showed high occurrences of mobile benthic decapods (3.03 ± 2.74 ind./min) and provided the first direct evidence that areas actively used by walrus in the Pechora Sea overlap with the distribution of the non-native omnivorous snow crab, *Chionoecetes opilio*.
5. Integrating multiple data sources provides an early foundation for the kinds of ecosystem-based approaches needed to improve Pechora Sea resource management and to underpin Russia's nascent marine spatial planning initiatives. Factors that need to be considered in marine spatial planning include impacts on benthic feeding grounds from offshore oil and gas development and the spread of the snow crab.

KEYWORDS
Arctic Ocean, Atlantic walrus, feeding grounds, macrobenthos, Pechora Sea, snow crab

1 | INTRODUCTION

1.1 | Atlantic walrus in the Pechora Sea

The Atlantic walrus, *Odobenus rosmarus rosmarus*, has an Arctic to sub-Arctic distribution from the eastern Canadian Arctic to the Kara Sea. Despite its wide distribution the subspecies has a relatively narrow ecological niche, and only specific areas provide both appropriate haulout sites and adequate foraging resources (Born, Gjertz, & Reeves, 1995). Atlantic walruses are benthic predators that predominately feed on bivalve molluscs (Born et al., 2003). Their full feeding cycle includes underwater foraging trips of up to 75 hr, followed by resting periods (Born et al., 2003). In winter, walruses haul out on sea ice; in summer, however, they require terrestrial haul-out sites near feeding grounds with large areas of shallow water and suitable bottom substrata to support productive macrobenthic communities (Wiig, Born, & Stewart, 2014).

In the Barents Sea, Atlantic walruses inhabit areas of Svalbard, Franz Josef Land, Novaya Zemlya, and the Pechora Sea (Wiig et al., 2014). The Pechora Sea is a relatively small, shallow semi-enclosed area in the south-east basin of the Barents Sea, experiencing significant sea ice for more than half of the year (Dobrovolsky & Zalogin, 1982). As of 2014, 4,000 heads (3,117 ± 1,210) were counted in the ice-free period in the Pechora Sea (Lydersen, Chernook, Glazov, Trukhanova, & Kovacs, 2012). The Pechora Sea population of walrus forms haul-outs on the Kolguev, Dolgy, Matveev, Golets, and Vaigach islands, combining into aggregations of up to 1,000 individuals on Vaigach and Matveev islands (Anufriev, Glotov, & Zolotoi, 2017; Lydersen et al., 2012; Semenova, Boltunov, & Nikiforov, 2015).

Besides the Pechora Sea providing important haulout sites for high-density aggregations, walruses here appear to form a semi-isolated, genetically unique group, with little to no movement elsewhere (Semenova, Boltunov, & Nikiforov, 2019). Genetic studies have revealed some low, yet significant differences in haplotype composition between the Pechora Sea walruses and those from the Svalbard–Franz Josef Land population, suggesting a degree of population differentiation (Andersen et al., 2017). Satellite tagging of 35 walruses in the Pechora Sea from 2012 to 2017 revealed that most animals resided in the Pechora Sea throughout the whole period, probably using marine habitats between Vaigach and Matveev islands as their key feeding grounds (Semenova et al., 2019).

1.2 | Pressures on walrus in the Pechora Sea

Historical pressures on walrus in the wider Barents Sea were confined to hunting. Any hunt of this subspecies in Russian waters has been prohibited since 1957 (Resolution of the Council of Ministers of the RSFSR no. 738(e); November 21,1956). Today, the Atlantic walrus subspecies is classified as an endangered species in the Red Data Book of the Russian Federation and as Near Threatened in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2019). Current threats to walruses are being posed by the encroachment of the offshore oil and gas industry and shipping sectors, as well as coastal developments, which create noise pollution and destroy important habitats (Boltunov, Belikov, Gorbunov, Menis, & Semenova, 2010; Semenova et al., 2019). The seabed of the Pechora Sea was, until recently, relatively undisturbed and there are no significant commercial fisheries in this region, unlike most of the Barents Sea (Bauch, Pavlidis, Polyakova, Matishov, & Koç, 1995; S. G. Denisenko, Denisenko, Chaban, et al., 2019). The Prirazlomnoye oil field began production in 2013 and remains Russia's first offshore oil-producing project on its Arctic continental shelf. It is located in the Pechora Sea approximately 50 km from the protected areas of Vaigach Island (Nature Park) and 30 km from Matveev Island (State Nature Reserve). As the rapid pace of climate change in the Arctic continues to accelerate alongside human activities, it is likely that Atlantic walruses will be further threatened by the predicted changes in the wider Arctic Ocean (Laidre et al., 2008). Therefore, in the Pechora Sea, it is likely that multiple stressors, including climate warming, loss of sea ice, retreating coastlines, noise pollution and habitat destruction, will have cumulative impacts on walrus haulout sites and benthic foraging resources.

The snow crab, *Chionoecetes opilio*, is a non-indigenous species in the Barents region recorded in fisheries by-catch since the mid-1990s, thereafter forming a self-producing population in the Barents Sea that is predicted to grow in size (Jørgensen & Spiridonov, 2013; Mullowney, Morris, Dawe, Zagorsky, & Goryanina, 2018). Snow crabs are benthic omnivores: active consumers with diverse flexible diets comprising a wide variety of prey types, including macrobenthos, fish and fishery discards, and other crustaceans (Squires & Dawe, 2003; Zalota, Spiridonov, & Vedenin, 2018). Invasive crustaceans pose an additional pressure on local macrobenthic communities that may result in reduced biomass and biodiversity, as has been shown for the king crab, *Paralithodes camtschaticus*, in Norwegian fjords (Oug, Cochrane, Sundet, Norling, & Nilsson, 2011). Therefore, the presence of the snow crab in the Pechora Sea poses a potential threat to the macrobenthos, including the foraging resources of walruses. There is currently no information on the diet of the snow crab in the Pechora Sea and trophic relationships between the Atlantic walrus and the snow crab remain unclear, and hence the snow crab may either compete with walruses over the native benthic communities or form an additional foraging resource for walruses.

1.3 | Walrus feeding behaviour and diet

It is critically important that the integrity of walrus benthic foraging resources is not diminished. The energetic needs of Atlantic walruses from Greenland showed that a single adult male spent approximately 100 hr in a full feeding cycle, with 75% of that spent foraging on benthic resources and 25% spent hauling out and resting on land (Born et al., 2003). An individual adult needs a daily gross energy intake of 200 kJ per kg body mass, i.e. a total quantity of food representing approximately 4–6% of its own weight, corresponding to 35–50 kg of macrobenthos (Born et al., 2003). Walruses are benthic foragers that actively consume bottom-dwelling invertebrates, specializing on bivalve molluscs (Born et al., 2003; Kastelein & Mosterd, 1989); however, their diet can include mobile benthic crustaceans, gastropods, and other invertebrates in both the Atlantic (S. G. Denisenko, Denisenko, Chaban, et al., 2019; Svetocheva & Semenova, 2017) and the Pacific subspecies (Chakilev & Kochnev, 2014; Fisher & Stewart, 1997). In an exceptional case from Svalbard, walrus have been documented to feed on flightless pink-footed geese *Anser brachyrhynchus* (Fox, Fox, Liaklev, & Gerhardsson, 2010) and seals (Born et al., 1995). To excavate burrowing bivalves from deep in the sediment, walruses have specialized morphological features: a 'digging' routing snout, with sensitive vibrissae and protected skin at the upper edge, and well-developed muscles in the head and neck (Kastelein & Mosterd, 1989). When searching for prey on the ocean floor walruses swim just above the bottom, with their head facing down, presumably using either vision or vibrissae sensation to search for prey items (Kastelein & Mosterd, 1989). Noise pollution and habitat destruction against a backdrop of climate change threaten the integrity of this specialized ecological niche, making it important that the locations and integrity of benthic foraging resources are documented, monitored, and conserved.

1.4 | Pechora Sea benthic communities

There are 712 macrobenthic invertebrate taxa recorded in the Pechora Sea, representing approximately 35% of the benthic species diversity of the entire Barents Sea (S. G. Denisenko, 2013). The relatively shallow depths of the Pechora Sea, the strong influence of continental run-off, and the mixture of water masses of Arctic and Atlantic origin mean that the benthic communities of the Pechora Sea mostly comprise boreal–Arctic species with a limnetic signature as a result of inputs from the Pechora River estuary (S.G. Denisenko, 2013). Communities are characterized by a relatively high faunal diversity and high variability in spatial distribution, presumably as a result of local environmental heterogeneity in seafloor topography and sediment type (Dahle, Denisenko, Denisenko, & Cochrane, 1998; S. G. Denisenko, Denisenko, Lehtonen, Andersin, & Laine, 2003). Macrobenthos of the Pechora Sea have been relatively well studied since the 1990s; however, there is still a mismatch between the number of sites from open-sea versus near-shore areas (N. V. Denisenko, Denisenko, & Lehtonen, 2019). Most of the benthic surveys in the area were conducted on board large research vessels, and the upper depth limit of these studies was about 10 m, resulting in near-shore shallow waters remaining massively under-reported. This is a common problem specifically for Arctic marine nature reserves because the outermost limits of these reserves rarely approach this depth (Gebruk et al., 2019). Therefore, benthic foraging resources for Atlantic walrus in the Pechora Sea have not been comprehensively studied because some of the key feeding grounds, such as those between Vaigach and Matveev islands (Semenova et al., 2019), are located in shallow waters. More recent attempts to address this have been undertaken at Dolgy Island (S. G. Denisenko, Denisenko, Chaban, et al., 2019; Sukhotin, Krasnov, & Galaktionov, 2008), but the macrobenthos from nearby Vaigach Island still remains poorly studied.

The main aim of the present study is to integrate multiple sources of environmental and biological data that have been collected over the last years by satellite telemetry, remotely operated vehicle (ROV), and benthic grab sampling to fill the gap in knowledge on the distribution and diversity of benthic foraging resources that support the Pechora Sea Atlantic walrus. The present study aims to: (i) identify key walrus feeding grounds; (ii) characterize the foraging resources in terms of macrobenthos abundance, biomass, diversity, and species composition; (iii) examine the distribution of mobile benthic fauna in walrus feeding grounds, potentially overlapping with walrus resource use; and (iv) estimate whether the area contains enough macrobenthic prey items to sustain the local Atlantic walrus population.

2 | METHODS

2.1 | Site description

Benthic surveys were conducted on board the RV *Kartesh* in July 2016, over an area of approximately 2,425 km^2, in the nearshore waters between the Vaigach, Matveev, and Dolgy islands, where the key terrestrial haulout sites of walruses are located in the Pechora Sea. Nineteen sites at a depth range from 9 to 66 m were assessed for diversity, biomass, and abundance of macrobenthic invertebrates (Figure 1; Table 1). The Matveev and Dolgy islands lie within the protected areas of Nenetsky State Nature Reserve, which also covers the marine area surrounding the islands. Vaigach Island, however, is classified as a nature park at the regional level; therefore, the protected area of the Vaigach Island does not expand to the nearby water territories (regional-level protected areas only apply to land).

2.2 | Data collection

2.2.1 | Benthic grab samples

Benthic grab samples were taken at 19 stations using the Okean-50 bottom grab, with a sampling area of 0.175 m^2. Bottom sediments

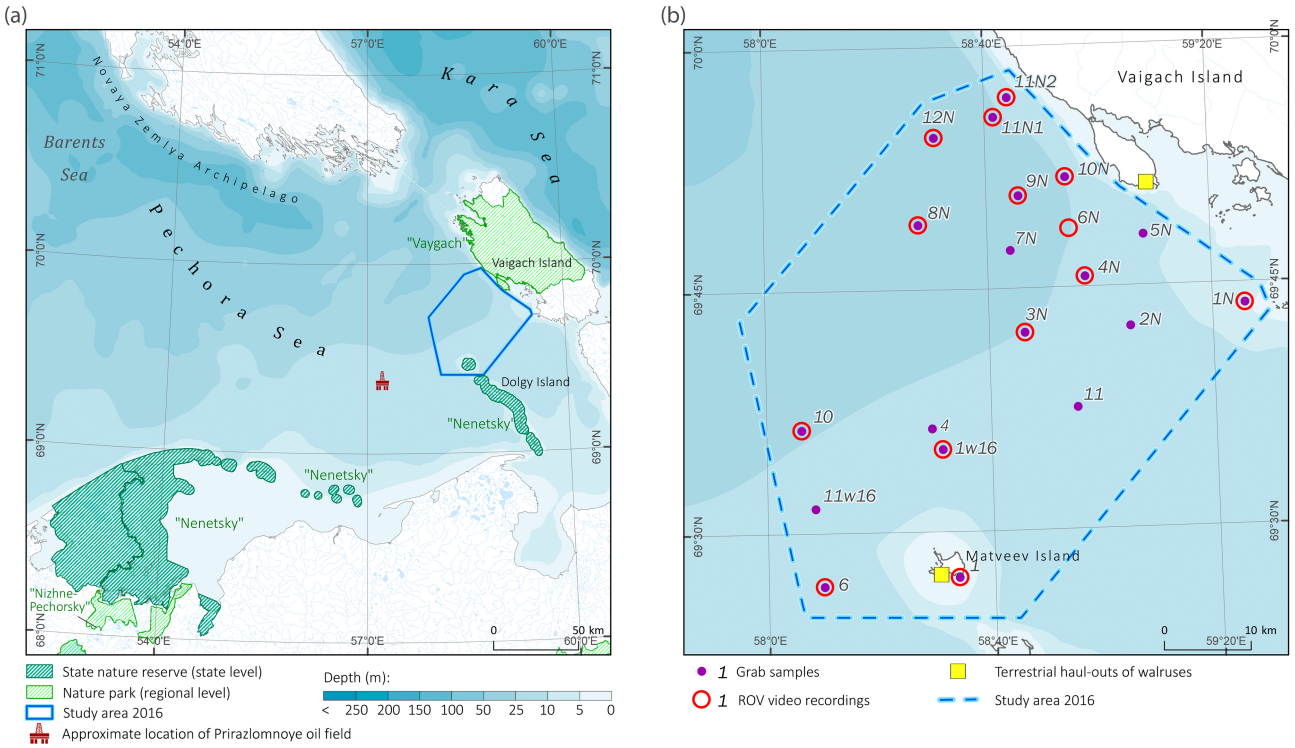

FIGURE 1 Overview of the study area: (a) co-location of the study area, key protected areas of the Pechora Sea, and Prirazlomnoye oil field; (b) sampling sites (Okean-50 benthic grab) and sites of ROV video recordings and locations of terrestrial haulout sites of walruses on Vaigach and Matveev islands

from the grab were washed over a 5-mm mesh with seawater. This mesh size was chosen to assess large macrobenthos that are likely to be the prey items of walruses. A 5-mm mesh is commonly used for commercial stock assessments, although it was shown that the use of smaller mesh sizes significantly decreases the loss of abundance of macrobenthos recorded in quantitative studies (Lubin, 2016). All macrobenthos were then fixed with 4% formalin solution and stored in labelled buckets.

In addition, a Sigsbee trawl (width 1 m, mesh 5 mm) was used for trawling assessment at stations 9N and 4N to verify the identification of benthic decapods. The trawl was towed for 20 min at each site at a maximum speed of 2 knots (approximately 1.1 m/s). Macrobenthic samples were rinsed with seawater and preserved in 4% formalin solution.

In the laboratory, all benthic samples were washed in freshwater, sorted, and then identified to the lowest possible taxonomic level using keys. Formalin-fixed benthos were sorted from the organic debris and re-fixed in 70% ethanol. All taxon names were standardized in accordance with the World Register of Marine Species (WoRMS). For each sample, taxa were counted and weighed on a jewellery scale (ML-CF3, SMARTron, China). Unidentified fragments were also weighed, recorded, and enumerated as 'Rest'. Polychaeta were removed from secretory tubes before counting, except for *Galathowenia oculata*: these were weighed in their tubes in order to prevent destroying the individuals. Bivalve molluscs and gastropods were weighed in their shells.

2.2.2 | ROV video recordings

Video recording was carried out from the vessel using the ROV Super GNOM Plus (Indel-Partner Ltd., Moscow, Russia). The ROV was equipped with two servo-driven video cameras (Super HAD 2 CCD; Sony, Tokyo, Japan), with tilt ±50°, a lighting complex synchronized with the camera (with 10 light-emitting diodes of 6,000 Lumens each), and a navigation system (with a course detector and depth sensor). Sixteen video transects were undertaken, of approximately 10 min each (counting from the moment the ROV reached the sea floor until the beginning of the ascent).

2.2.3 | Satellite tracking data

Position data from satellite-linked radio transmitters were gained through a complex study of movement patterns of walruses in the Pechora Sea in 2012–2017; the full description of the method is given in Semenova et al. (2019). Adult male walruses were tagged with satellite-linked radio transmitters (platform terminal transmitters, PTTs), designed and manufactured in Russia. The transmitters provided position data received through the Advanced Research and Global Observation Satellite (ARGOS) system. The tags had a 'wet/dry' sensor and were programmed to transmit only in the 'dry' mode to save battery life. PTTs were mounted on the walruses with the help of stainless-steel pivoting harpoons. The harpoon tip was

TABLE 1 List of sampling sites (Okean-50 benthic grab, with a sampling area of 0.175 m^2) and sites of ROV video recordings studied in the Pechora Sea in July 2016, with coordinates and depths (m)

	Coordinates					
Site number	N	E	Grab sampling	Trawl sampling	ROV video recordings	Depth (m)
1	69°27.180′	058°33.651′	+		+	23
4	69°36.411′	058°29.422′	+			30
6	69°26.734′	058°09.816′	+		+	26
10	69°36.436′	058°06.222′	+		+	25
11	69°37.565′	058°55.394′	+		+	25
1w16	69°35.115′	058°31.242′	+		+	28
11w16	69°31.553′	058°08.465′	+			25
1N	69°43.718′	059°25.786′	+		+	25
2N	69°42.509′	059°05.248′	+			26
3N	69°42.259′	058°46.335′	+		+	28
4N	69°45.635′	058°57.347′	+	+	+	30
5N	69°48.155′	059°08.034′	+			23
6N	69°48.647′	058°54.712′			+	41
7N	69°47.342′	058°44.148′	+			27
8N	69°49.034′	058°27.683′	+		+	40
9N	69°50.727′	058°45.804′	+	+	+	39
10N	69°51.818′	058°54.302′	+		+	29
11N1	69°55.629′	058°41.640′	+		+	32
11N2	69°56.821′	058°44.182′	+		+	66
12N	69°54.413′	058°30.867′	+		+	44
ROV6	69°51.470′	059°11.691′			+	8.7

Note: for the ROV video recordings, the coordinates and depths were taken at the moment when the ROV reached the sea floor and the recording started.

TABLE 2 Date of first and last locations, total duration of study, and number of days with transmission for seven walruses tagged and studied in 2016

Walrus ID	Date of the first location	Date of the last location	Duration (days)	Number of days with transmission
01_2016	July 13, 2016	July 22, 2016	9.5	9.5
02_2016	July 13, 2016	October 7, 2016	85.5	83
03_2016	July 11, 2016	August 9, 2016	29	16
04_2016	July 11, 2016	August 8, 2016	28	28
05_2016	July 13, 2016	August 18, 2016	36	30.5
06_2016	July 13, 2016	July 31, 2016	18	13
07_2016	July 11, 2016	August 18, 2016	38	34.5

thrust through the skin of a sleeping walrus with the help of a 3-m-long wooden pole. The walruses were not immobilized. For the present study, only data collected in July–October 2016 were used so that benthic foraging resources were assessed for the area where walruses spent most time in the summer of 2016 (Table 2). Seven adult male walruses were tagged at the haulout site on Vaigach Island (Semenova et al., 2019) and their movement tracks were analysed to identify areas of the highest density of movements of walruses (potential feeding grounds).

2.3 | Data analysis

All calculations were performed using the free statistical software package PAST 3.22 (Hammer & Harper, 2006; Hammer, Harper, & Ryan, 2001).

Mean values ± standard errors were measured for biomass (g/m^2) and abundance ($ind./m^2$). Standard indices, including dominance, Simpson index, and Shannon index, were used to characterize the diversity of macrobenthos in the area, based on abundance data. To

assess predicted species richness ($\tilde{S}$) in the research area, a species accumulation curve was calculated using the Chao-2 richness estimator, as follows:

$$\tilde{S} = S_{obs} + \frac{(H-1)s_1^2}{2Hs_1},$$

where H is the number of samples, S_{obs} is the total number of observed species, and s_1 is the number of species found in exactly one sample.

The biomass of macrobenthos was used to characterize the foraging potential of the research area for walruses. Types of macrobenthic communities were defined by biomass data. The species with the highest biomass at stations were considered dominant; the second, third, and fourth most abundant species were considered subdominant. Non-metric multidimensional scaling (nMDS) based on the Bray–Curtis similarity index was used for the analysis. To define types of communities, the cluster analysis based on an unweighted pair group method with arithmetic mean (UPGMA) algorithm with Bray–Curtis similarity index was used. To assess the significance of differences between the clusters identified by the nMDS and UPGMA methods, a pairwise analysis of similarities (ANOSIM) was performed. The P values of each pair were given, with sequential Bonferroni corrections applied.

The ROV video recordings were analysed using open-source VLC MEDIA PLAYER software. All mobile benthic decapods were counted and where possible identified to the species or genus level. The occurrences of decapods per minute (ind./min) on video recordings were then calculated as the total number of mobile benthic decapods (including decapods not identifiable to species level) divided by the duration of time of the video transect from the moment the ROV reached the seabed until the start of the ascent, excluding non-readable fragments of video recordings (i.e. where the seabed was not

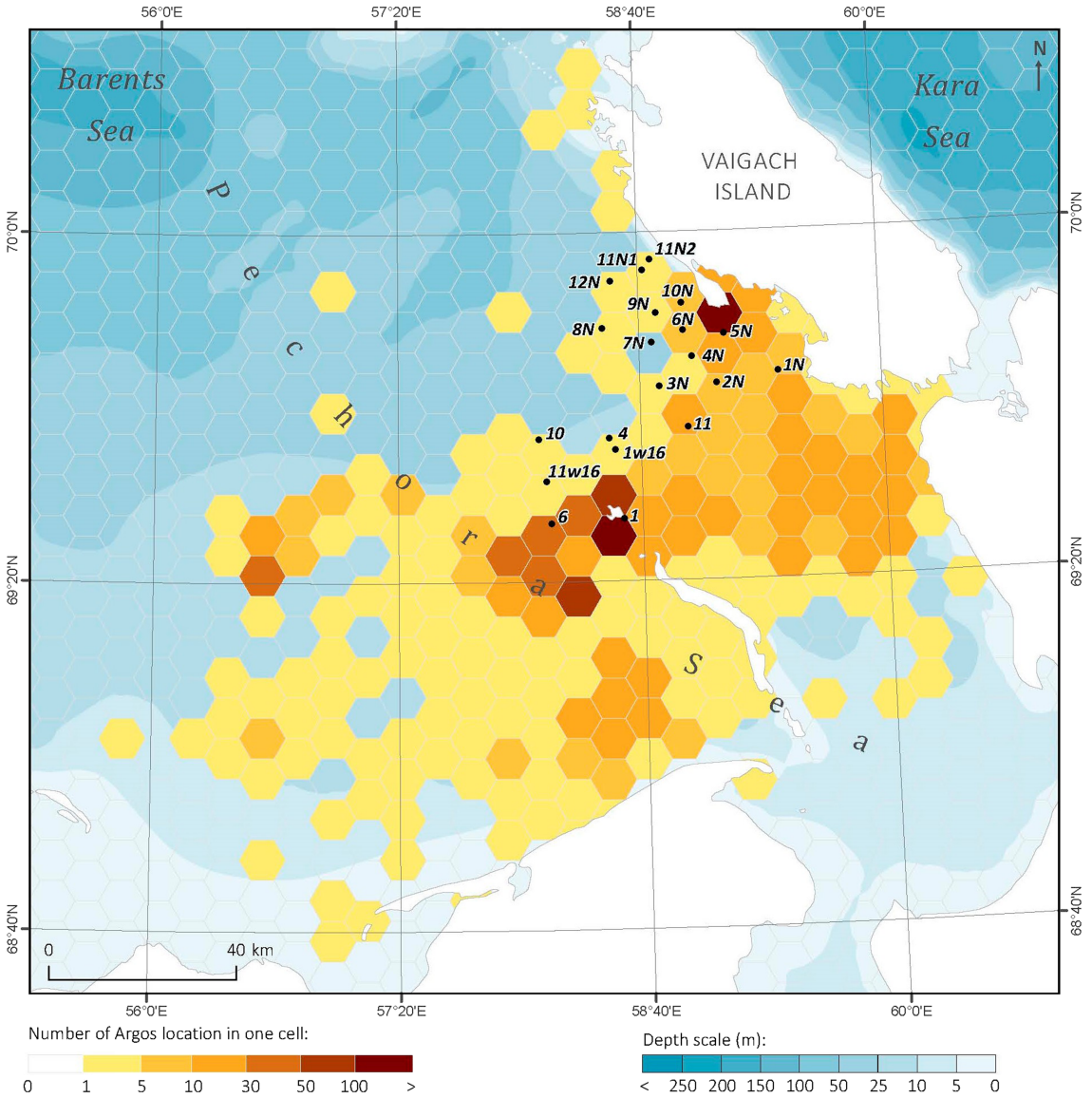

FIGURE 2 Movements of walruses in the research area in 2016. The number of ARGOS locations are shown for each cell on a scale from 0 to >100. Areas of greatest density (near Matveev Island and Cape Lyamchin Nos, Vaigach Island) are shown in brown

visible) and when the camera was stationary (Mokievsky, 2015). Pearson's *r* correlation was used to define statistically significant ($P < 0.05$) correlations between macrobenthic biomass in grab samples and decapod occurrence based on ROV video recordings.

The telemetry positions data of seven tagged walruses were received from ARGOS. Walrus location maps were generated using ARCMAP 10.4.1. Walrus distribution was calculated using a hexagonal grid with 5-km cell edge and the reference coordinate system UTM/WGS84 Zone 40 N.

3 | RESULTS

3.1 | Areas of high walrus density

Walrus location data in the summer of 2016 were obtained from seven tags. All walruses remained within the Pechora Sea for the duration of the study (from July 11, 2016 to October 7, 2016). The number of days with transmission for each walrus varied from 9.5 to 83, with an average of 35 ± 12.34 days per walrus. To assess the areas of highest density, the number of ARGOS locations was calculated for each 5-km cell (Figure 2). The high-density areas included the terrestrial haul-out sites on Matveev Island and Cape Lyamchin Nos (Vaigach Island), and in the waters between the islands (Figure 2).

3.2 | Benthic communities

A total of 131 taxa of macrobenthic invertebrates were found in the samples, 106 of which were identified to species level. Full list of species with biomass and numbers for each species per station provided in supporting information. The most diverse groups were polychaetes (84 taxa, 68 species), molluscs (20 taxa, 19 species), and crustaceans (12 taxa, 10 species). Other taxonomic groups, including bryozoans, cnidarians, echinoderms, nemertean, priapulids, pycnogonids, and sipunculid worms were represented in minor proportions. The mean species richness was 21.57 ± 8.68, ranging from eight to 41 taxa per station. The total number of species predicted for the area by the Chao-2 estimator was 204 ± 28, and hence the species accumulation curve was approaching the saturation level but did not reach it (Figure 3). High values of the Simpson diversity index (0.8 ± 0.1, on a scale of 0 to 1) indicated heterogeneous communities with a low dominance of single taxa ($D = 0.19 \pm 0.1$). Communities overall exhibited a relatively high Shannon entropy index (2.26), i.e. communities contain many taxa, but each are represented by only a few individuals (Hammer & Harper, 2006).

The mean abundance was 370 ± 14 ind./m^2, ranging from 86 ± 3 ind./m^2 (station 1) to 869 ± 30 ind./m^2 (station 10). The mean biomass was 147.11 ± 7.35 g/m^2, ranging from 10.57 ± 0.41 g/m^2 (station 7N) to 693.47 ± 39.87 g/m^2 (station 9N). The bivalve molluscs *Astarte borealis*, *Astarte montagui*, and *Ciliatocardium ciliatum* together comprised 66% of the total biomass, accounting for 30, 21, and 15%, respectively (Figure 4). All other taxa contributed less than 10% each to the total biomass, with 118 taxa contributing less than 1% each.

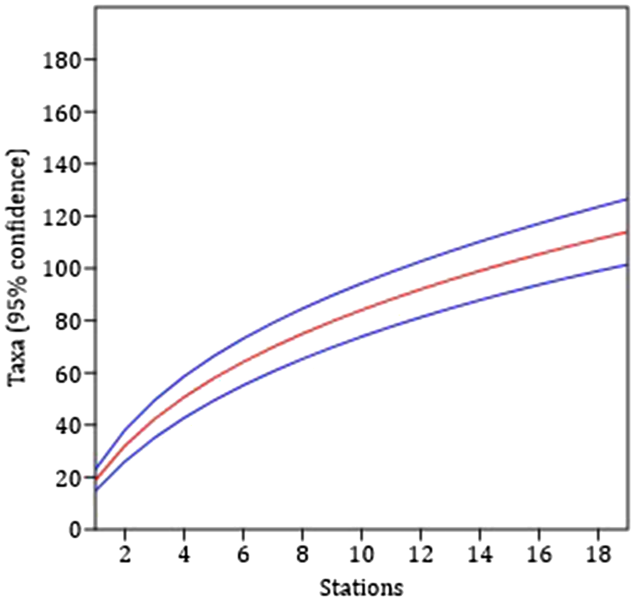

FIGURE 3 Sample rarefaction curve: the red line plots the accumulated number of species; the blue lines delineate the 95% confidence interval

The clustering and MDS revealed four groups of stations in the study area: group 1, *A. borealis* community; group 2, *A. montagui*–*Macoma calcarea* community; group 3, *C. ciliatum* community; and group 4, macrobenthos with low biomass and various dominants, including the polychaete *Hamingia arctica*, the bivalve *Yoldia hyperborea* and solenogasters (Figure 5). Group 1 was strongly dominated by *A. borealis* (stations 8N, 9N, 10N, and 1w16 in the northwest and central areas); it had the highest mean biomass (289.73 ± 14.94 g/m^2) and a total of 65 taxa, the maximum among all the stations (ranging from 18 to 41 per station). Stations within group 2 (stations 10, 12N, 11N2, 7N, 3N, 11N1, and 4N) were dominated by *A. montagui* and *M. calcarea*, with various subdominants, including *Y. hyperborea*, *Nephtys ciliate*, and *Golfingia margaritacea*. Group 2 was characterized by a low mean biomass (41.05 ± 1.5 g/m^2) and by high species richness ($n = 74$; 14–34 per station). Group 3 (stations 6, 11w16, 4, 11, and 1N) was mainly concentrated in the shallow waters in the south-east area close to Matveev Island. The biomass was formed by large bivalves, *C. ciliatum* and *Serripes groenlandicus*, with contributions from *A. montagui* and *Ophelia limacina*. Group 3 was characterized by a high biomass (248.5 ± 12.95 g/m^2) and a relatively low richness ($n = 60$; 15–30 per station). The remaining three stations (stations 1, 2N, and 5N) formed poly-dominant group 4, with the lowest biomass (35.48 ± 1.5 g/m^2) and richness ($n = 47$; ranging from nine to 27 per station). In terms of biomass, the dominants were *Pectinaria hyberborea*, *H. arctica*, and *Y. hyperborea* for stations 1, 2 N and 5 N, respectively.

The total biomass (g/m^2) and proportions of dominant and subdominant species for each station are shown in Figure 6.

The four types of macrobenthic communities revealed by nMDS and clustering analysis showed little statistical difference, according to

the ANOSIM test: groups 1 and 2 and groups 2 and 3 were statistically significantly different ($P < 0.05$, Table 3), but not the others.

Macrobenthos in the research area was highly heterogeneous. The biomass and species composition per station varied greatly: species dominating the biomass were different at 62% of the stations. The overall macrobenthos biomass in the area, however, was dominated by three species of bivalve molluscs: *A. borealis* (30% of the total biomass), *C. ciliatum* (21%), and *A. montagui* (15%). In general, macrobenthos in the research area were formed by a highly heterogeneous community of bivalves, *A. borealis*–*C. ciliatum*, with variable dominants and subdominants at each station.

3.3 | Mobile benthic decapods

Video footage obtained at 15 transects was studied for the presence of mobile benthic fauna. The following mobile benthic invertebrates were recognized on the video recordings: the snow crab *C. opilio*, the

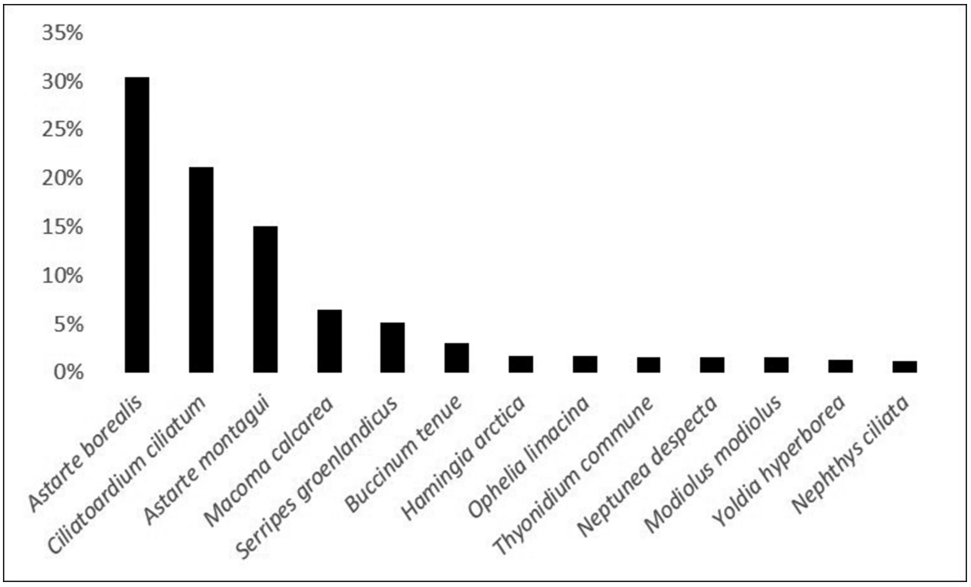

FIGURE 4 Species contribution (%) to total biomass (g/m^2) of macrobenthos in the area: 13 species with >1% contribution are presented

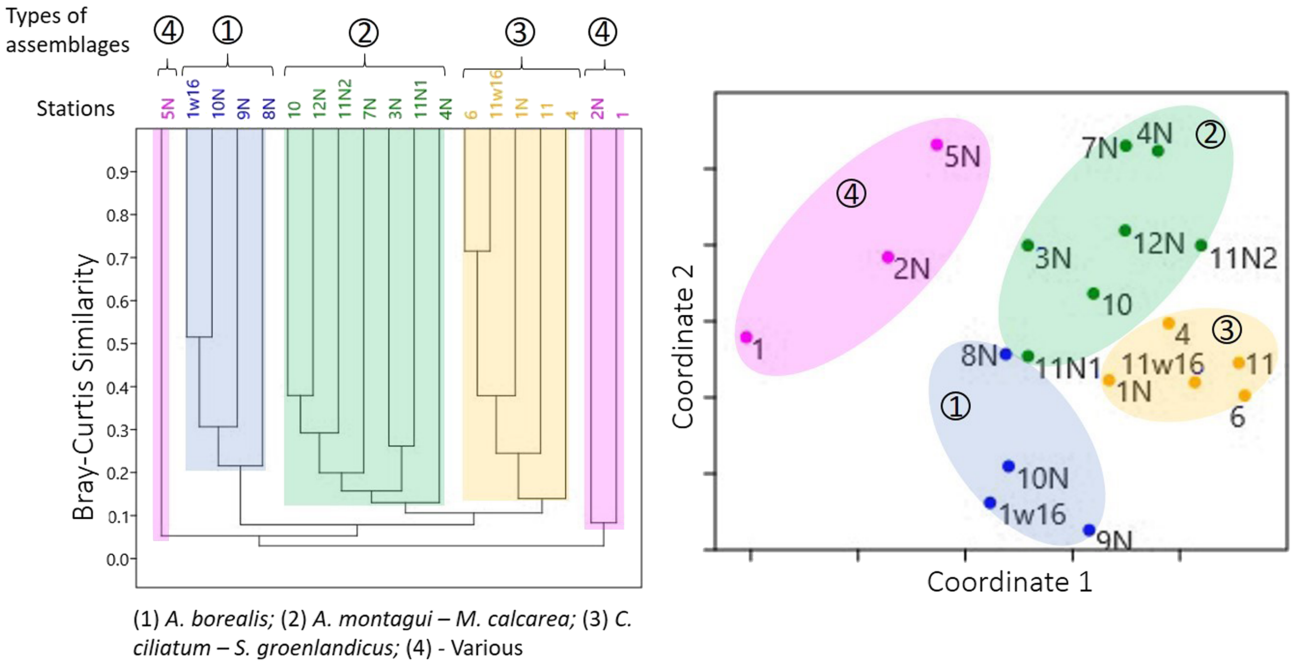

FIGURE 5 Groups of stations based on UPGMA hierarchical cluster analysis (on the left) and nMDS (on the right), both calculated with the Bray–Curtis similarity measure: group 1, 1w16, 10N, 9N, and 8N, *Astarte borealis* community; group 2, 10, 12N, 11N2, 7N, 3N, 11N1, and 4N, *Astarte montagui–Macoma calcarea* community; group 3, 6, 11w16, 4, 11, and 1N, *Ciliatocardium ciliatum–Serripes groenlandicus* community; group 4, 5N, 2N and 1, various dominants

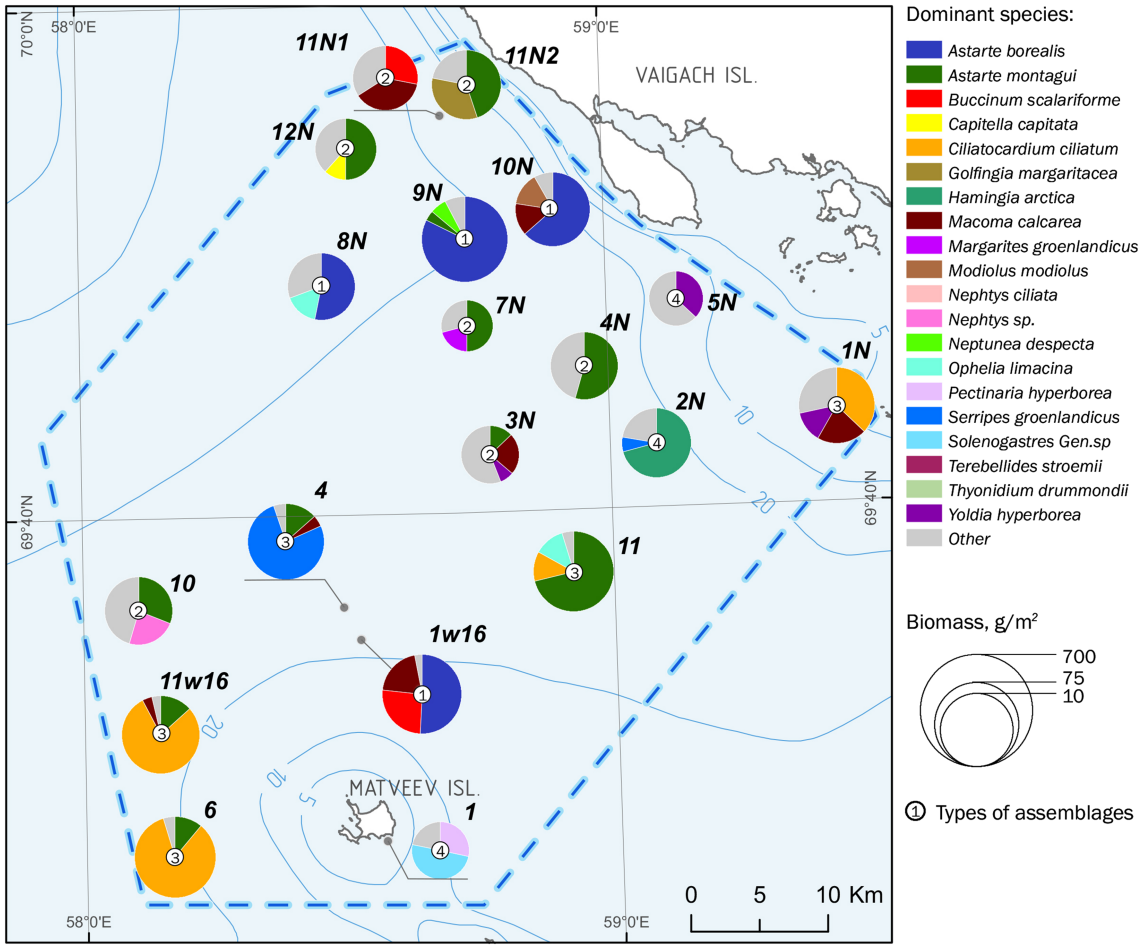

FIGURE 6 Macrobenthic diversity in the research area: the species composition and biomass for each station are shown in the pie charts proportional to total biomass per station (dominant and subdominant in biomass species shown by different colours, with the list of species provided in the legend). The number in the centre of the pie chart shows the type of macrobenthic assemblage

TABLE 3 Pairwise comparison of groups of stations with ANOSIM analysis and *P* values, and with sequential Bonferroni significance shown by green shading

	1	2	3	4
1				
2	*P* = 0.01; *r* = 0.62			
3	*P* = 0.09; *r* = 0.19	*P* = 0.01; r = 0.65		
4	*P* = 0.48; *r* = 0	*P* = 0.81; *r* = −0.29	*P* = 0.764; *r* = −0.2	

spider crab *Hyas araneus*, the hermit crab *Pagurus pubescens*, and unidentified decapods. Species identification was confirmed by trawl samples taken at stations 9N and 4N. A total of 255 mobile benthic decapods were recorded in video transects (Table 4). Hermit crabs were the most abundant decapods in the area, accounting for >65% of the total number, with snow and spider crabs being equally present, accounting for approximately 13% each. The average decapod occurrence was 3.03 ± 2.74 ind./min, ranging among stations from 0.65 to 11.67 ind./min. Noticeably, at least one decapod was present in each recording. Values of decapod occurrence were highest at stations 11N2, 11N1, and 12N in the northeast of the research area, closest to the shoreline of Vaigach Island, whereas sites 1 and 6 to the south of Matvev Island showed the lowest values. Occurrences of each species and the contribution of decapod species to overall occurrences are illustrated in Figure 6. There was no statistically significant correlation between macrobenthic biomass and crab occurrence (Pearson's correlation coefficient $r = -0.07$, $P > 0.05$), nor any positive or negative correlation between the two crab species *C. opilio* and *H. araneus* ($r = 0.04$, $p > 0.05$).

4 | DISCUSSION

All recorded walrus movements in 2016 were within the Pechora Sea, with the areas of highest use lying between the haul-out sites of Vaigach and Matveev islands. This area was also identified as very likely to be a key feeding ground of the walruses in the Pechora Sea, according to the results of a recent 5-year telemetry study (Semenova et al., 2019). We suggest that the satellite footage of walrus

TABLE 4 Main characteristics of ROV video recordings: start coordinates; total number of benthic decapods; number of each species; duration of 'meaningful time' (excluding non-readable fragments of video recordings, where the seabed was not visible, and when the camera was stationary); and overall crab occurrence, ind./min

Start coordinates		Total decapods, *n*	*C. opilio*, *n*	*H. araneus*, *n*	*Pa. pubescens*, *n*	Decapoda, *n*	Meaningful times, sec	Occurrence, ind./min
N	E							
69°27.195′	058°33.672′	6	2	2	1	1	551	0.65
69°26.737′	058°09.819′	6	1	0	4	1	350	1.03
69°36.440′	058°06.223′	12	3	1	6	2	475	1.51
69°35.115′	058°31.236′	10	4	1	3	2	329	1.82
69°51.470′	059°11.691′	4	1	3	0	0	178	1.35
69°43.719′	059°25.806′	7	0	2	3	2	276	1.52
69°42.249′	058°46.377′	14	0	0	14	0	568	1.48
69°45.640′	058°57.334′	19	2	5	12	0	410	2.78
69°48.647′	058°54.712′	26	5	3	17	1	464	3.36
69°51.840′	058°54.339′	21	2	2	16	1	534	2.36
69°50.728′	058°45.817′	33	2	9	21	1	476	4.16
69°49.034′	058°27.680′	17	2	2	11	2	478	2.13
69°54.414′	058°30.867′	34	3	2	28	1	489	4.17
69°55.629′	058°41.637′	25	4	2	16	3	274	5.47
69°56.819′	058°44.136′	21	3	0	17	1	108	11.66

movements within a relatively small area for the whole duration of the study (83 days) can be used as circumstantial evidence of foraging activity of walruses in the area. Cells with maximum ARGOS locations (>100 locations per 5-km hexagonal cell) occurred near benthic stations 1 and 5 N, characterized by the lowest biomass of macrobenthos across the study area (<20 g/m^2). Stations 6, 11, and 9N, with the highest biomass of foraging macrobenthos, were characterized by moderate to low numbers of ARGOS locations, ranging from 1 to 50. In general, all seven tagged walruses regularly moved within the study area for the whole duration of the study, with most of their movements concentrated near the haul-out sites of Vaigach and Matveev islands.

Considering the high conservation status of the Atlantic walrus in the Pechora Sea, the relative isolation of the Pechora walruses, and potential impacts of human activities in the area, it is crucial to identify and study the key habitats of this species. Feeding grounds are one of these key habitat types. Noticeably, areas that are likely to be the feeding grounds of the walruses lie outside the protected zones of Nenetsky Nature Reserve and Vaigach Nature Park, and are considerably closer to the areas of active offshore oil exploration and production (approximately 60 km from the Prirazlomnoye oil field). We suggest that both natural and anthropogenic factors need to be considered as potential drivers of changes in macrobenthic biomass in the area. Long-term environmental monitoring needs to be undertaken to detect these changes, including an annual benthic survey at an established network of stations, supported by ROV assessments of mobile benthic fauna, observations of walrus abundance and movement, and diet analyses of walrus scat. This will constitute an essential first step for developing a more comprehensive understanding of ecosystem dynamics that can then contribute towards marine spatial planning for the area.

Macrobenthos within walrus feeding grounds were formed by a highly heterogeneous community of bivalves *A. borealis*–*C. ciliatum* with variable dominants and subdominants at each station (mean biomass of 147.11 ± 7.35 g/m^2 and mean abundance of 370 ± 14 ind./m^2). Similar results were shown in the most recent benthic survey near Dolgy and Matveev islands, based on data collected in 2014 and 2016 (S. G. Denisenko, Denisenko, Chaban, et al., 2019). Within the relatively small research area, these authors described five types of macrobenthic communities mainly dominated by bivalves, with the most extensive community dominated by *A. borealis* and *M. calcarea*. The biomass of macrobenthos in 2016 varied from 14.5 ± 6.6 to 363 ± 132 g/m^2 (S. G. Denisenko, Denisenko, Chaban, et al., 2019), with values noticeably smaller than in the present study: ranging from 10.57 ± 0.41 to 693.47 ± 39.87 g/m^2. This is probably a result of the smaller grab used by S. G. Denisenko, Denisenko, Chaban, et al. (2019): 0.1 m^2 compared with 0.175 m^2 in the present study. The list of dominant species in S. G. Denisenko, Denisenko, Chaban, et al. (2019) also differed from our results. According to these authors, the following species contributed most to the overall biomass: *Mytilus edulis*, *Mya pseudoarenaria*, *S. groenlandicus*, *Semibalanus balanoides*, *Balanus balanus*, *M. calcarea*, *Hyas coarctatus*, *Cistenides hyperborean*, and *Buccinum undatum*. Only two of these species, *S. groenlandicus* and *M. calcarea*, appeared in the list of dominants in the present study.

The macrobenthos of the Pechora Sea is relatively well studied, but very limited benthic surveys have been conducted inside the research area in the shallow waters near Vaigach Island. According to the most complete review of macrobenthos of the Pechora Sea by

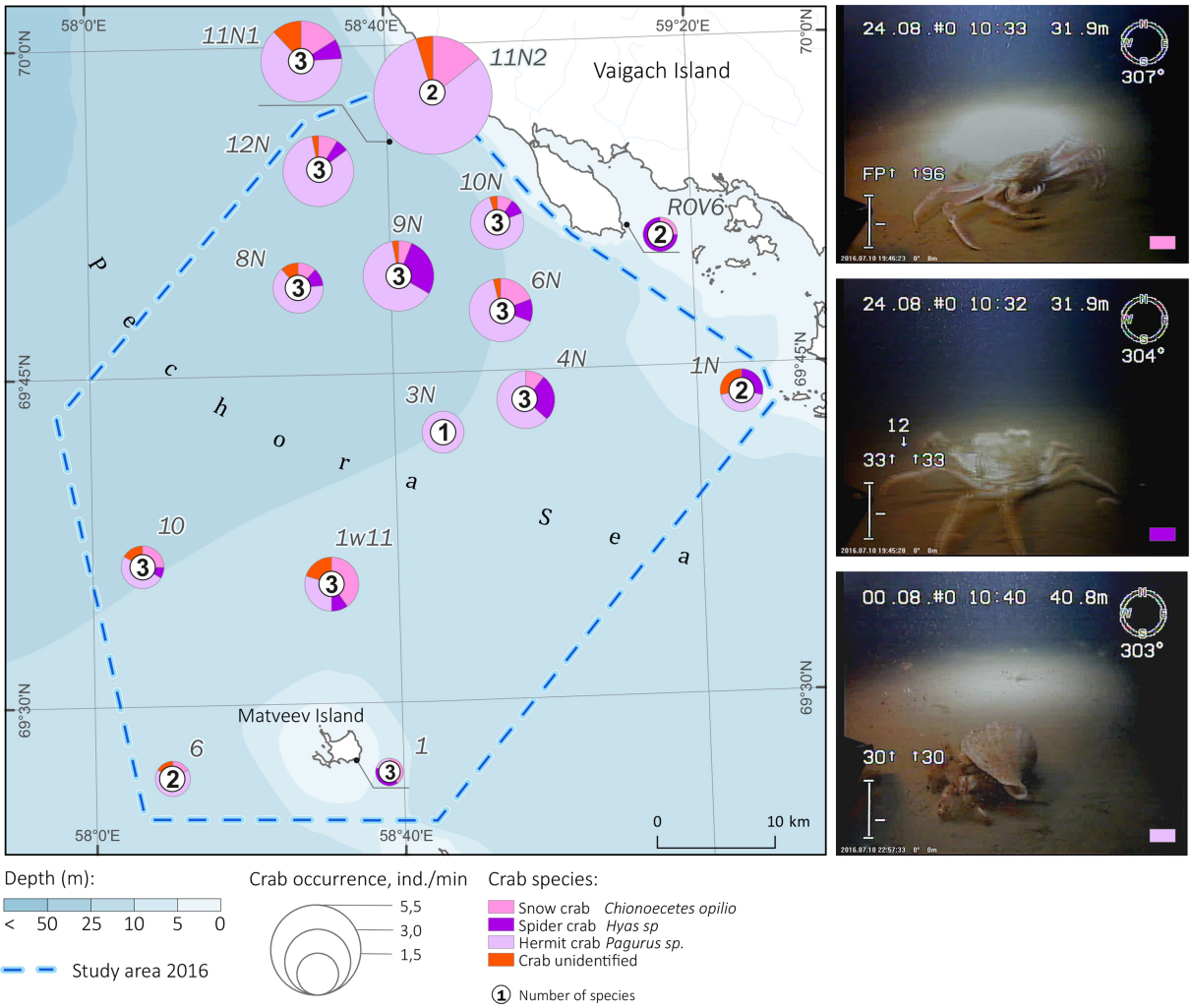

FIGURE 7 Occurrence of mobile benthic decapods (ind./min) on 16 ROV video recordings in July 2016 in the Pechora Sea. Pie charts show species composition by different colour sectors and are proportional to crab occurrence, ind./min

S. G. Denisenko (2013), considering all data collected from 1920 to 1990, the present research area falls into the zone where the community *Spiochaetopterus typicus–A. borealis* (type 8) alternates with the community *S. groenlandicus* (type 9). Only one station of this survey was located within the research area, however, and hence it is not surprising that more dense sampling in the present study revealed a highly mosaic community, with different dominants. Remarkably, in the present study *A. borealis* and *S. groenlandicus* remained on the list of dominants, whereas *S. typicus* was still present in the area with 10% occurrence across our sampling sites but did not form a large enough stock to be recognized as one of the dominants by biomass. It was previously discussed in the literature that a significant reduction of biomass of the stenothermal species *S. typicus* is the most common trend in the Russian Arctic and could either be a result of climate change or arise from different approaches to quantifying organisms in the samples (Zhirkov, 2001).

Overall, a macrobenthic community with a mean biomass of 147.11 ± 7.35 g/m^2 was available for the walruses in our research area in 2016, based on grab sampling. Previous diet studies showed that bivalves were the predominant prey items of Atlantic walruses (Born et al., 2003; Fisher & Stewart, 1997; Gjertz & Wiig, 1992). We can therefore speculate that bivalve molluscs, *A. borealis*, *C. ciliatum*, and *A. montagui*, formed the bulk of the foraging biomass available for walruses in the area.

In addition, ROV video recordings showed 100% occurrence of mobile benthic decapods in the area, with at least one specimen per recording, and with an average crab occurrence of 3.03 ± 2.74 ind./min (Figure 7). Of the three benthic decapod species identified in the video recordings, *H. araneus* and *Pa. pubescens* were also found in the grab samples; however, the snow crab *C. opilio* was only observed in the video recordings and trawls. The present study is the first evidence of an overlap between areas of high density of walruses and the distribution of the snow crab in the Pechora Sea. We suggest that comparative studies of regional diets of both species are needed to further reveal any possible interactions. In particular, scat samples of the walruses should be studied specifically for the traces of DNA from the snow crab to investigate whether the new invader forms an additional feeding resource for walruses. First data on morphological analyses of the 16 scat samples collected from 2013 to 2016 from the Vaigach, Matveev, and Novaya Zemlya islands revealed 10 prey items,

including *Astarte* sp., *Buccinum* sp., *Cardium* sp., *Cryptonatica affinis*, *Hiatella arctica*, *Lycodes sp*., *Mya* sp., *Nuculana pernula*, *Sclerocrangon* sp., and *S. groenlandicus* (Svetocheva & Semenova, 2017). Visual identification of the fragments from the scat samples provide valuable insights into the diets of walruses; however, clearly there are some limitations both in taxonomical resolution of identification and in estimating the biomass of the prey items based on the partly digested fragments. We suggest that visual analyses of scat samples should be combined with molecular analyses, including DNA isolation using specific primers to investigate traces of species in diets, supported by comprehensive benthic surveys to assess the available biomass of benthic resources.

Considering consumption rates are estimated at nearly 50 kg of wet-weight biomass of bivalves per individual walrus daily (Born et al., 2003) and the observed population of 1,000 heads on the Vaigach and Natveev island haul-out sites (Semenova et al., 2015), the macrobenthos in the area are clearly under massive pressure from walruses as a result of direct consumption and habitat destruction during foraging trips. Observations of benthic food resources for walruses in Svalbard coastal waters formed by Bivalvia and Decapoda (Węsławski, Hacquebord, Stempniewicz, & Malinga, 2000) led to the conclusion that if conservative estimates for walrus consumption rates were applied, the observed population of walruses in Svalbard waters should have taken the entire production of bivalve molluscs. Using the same assumptions, that the average weight of a male walrus is approximately 1,000 kg and the daily food intake of a walrus accounts for 5.7% of their body weight (Węsławski et al., 2000), it is estimated that the walruses observed on the Vaigach–Matveev haulouts (1,000 heads) require 57 tons of food daily, 4,731 tons for the duration of the study (83 days), or 20,805 tons per annum. Given the relatively low biomass of macrobenthos in the area (147.11 ± 7.35 g/m^2), the low production/biomass ratio of bivalves, estimated as 0.1 (Petersen, 1989), and the presence of other benthic predators in the area, then (i) consumption rates of walruses known from literature are not entirely accurate; (ii) there might be additional foraging resources in the area that are not captured by grab sampling; or (iii) walruses use resources from additional feeding grounds. Similar conclusions were made for the Svalbard walruses, where Węsławski et al. (2000) hypothesized the presence of biological hot spots in the area with extremely high benthic biomass. In the Pechora Sea, such hot spots can be formed by blue mussels, as evident for Dolgy Island (Sukhotin et al., 2008), or by burrowing molluscs such as *Mya truncata*, but further observations with different sampling techniques are needed to estimate the biomass of these species.

The Nenetsky Nature Reserve also provides important foraging grounds for marine ducks, including the king eider (*Somateria spectabilis*) and the black scoter (*Melanitta nigra*). Both species together form summer gatherings that may exceed 10,000 individuals on Dolgy Island from mid-July to mid-October, to feed and moult before migrating to wintering grounds (Sukhotin et al., 2008). Eiders, like Atlantic walruses, are specialized benthic predators feeding on marine invertebrates and specifically bivalves (Born et al., 2003; Sukhotin et al., 2008). The present study revealed an additional benthic predator (omnivore) present in the same area, the snow crab, that could impose an additional pressure on the local macrobenthos. Altogether, walruses, marine ducks, and benthic decapods are likely to feed on macrobenthos in the area between Vaigach and Matveev islands, with their numbers increasing significantly over the summer period. At this point it is hard to argue whether macrobenthos in the area provides enough foraging biomass to sustain the observed populations of benthic predators. We estimate the foraging capacity of the area as an average of 147.11 ± 7.35 g/m^2, which is by far the most precise evaluation of macrobenthic biomass in the area (with a 5% standard error). To reveal the impacts of all factors listed above as well as increasing water temperature (S. G. Denisenko, Denisenko, Chaban, et al., 2019), further estimations of macrobenthic biomass and its dynamics are needed in the area of the feeding grounds of walruses. We suggest using our knowledge of the basic prey items of walruses in the region when choosing approaches for future studies. The biomass of key prey items, including *A. borealis*, *C. ciliatum*, and *A. montagui*, can be used as an indicator parameter of foraging capacity of the area in future studies. The study area is likely to constitute an important feeding ground for the walruses; however, the system of protected areas that is currently in place in the Pechora Sea was developed based on land-sourced data, and important factors such as the distribution and biomass of benthic foraging resources were not taken into consideration. Establishing a long-term environmental monitoring programme to observe the dynamics of biomass along with walrus behaviour and density would provide a foundation for the kinds of ecosystem-based approaches needed to improve Pechora Sea resource management and to underpin Russia's nascent marine spatial planning initiatives.

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ORCID

Anna Gebruk https://orcid.org/0000-0002-2516-8286
Varvara Semenova https://orcid.org/0000-0003-3387-0814
Lea-Anne Henry https://orcid.org/0000-0001-5134-1102
Bhavani E. Narayanaswamy https://orcid.org/0000-0002-5810-9127

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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